AEOLID NUDIBRANCHS AS PREDATORS AND PREY

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ABSTRACT

The biology and autecology of aeolid nudibranchs are much better known than are the roles nudibranchs play in the communities in which they occur. This report describes known and potential roles aeolid nudibranchs play as both predators on cnidarians and other taxa and as prey to higher trophic level predators.

Aeolid nudibranchs are well-known predators of sessile cnidarians, particularly hydroids, anemones and corals (Hyman, 1967). There is an extensive literature on the systematics (i.e. McDonald, 1986), biology and ecology of aeolids (Swennen, 1961; Miller, 1961, 1962; Thompson, 1964; Thompson and Brown, 1984; Harris, 1973; Clark, 1975; Nybakken, 1974, 1978; Todd, 1981, 1983). The two recent reviews by Todd (1981, 1983) summarize much of what is known about the ecology and reproductive biology of nudibranchs. This information relates primarily to the autecology of the group, particularly locality and seasonality data and information on food preferences. Few studies have focused on the potential roles of aeolid nudibranchs within the communities in which they exist. This is equally true of their roles as both predators and as prey. The information that is available suggests aeolid nudibranchs can play significant parts in communities occupying hard substratum. The purpose of this report is to describe aspects of aeolid ecology that indicate their possible impact on the communities in which they occur and to speculate on the mechanisms by which they influence community development and organization. The emphasis will be first on nudibranchs as predators and then as prey.

AEOLIDS AS PREDATORS

Most aeolid nudibranchs are partial predators consuming portions of colonial prey such as hydroids, octocorallian and scleractinian corals (Todd, 1981). Even many anemone-eating species feed on anemones that form aggregations or clones or are too large as individuals to consume in a single meal. This mode of predation has several implications for prey species populations: (1) physical gaps in the colony, aggregation or clone can be formed; (2) the population structure of the prey can be altered; and (3) the prey can respond by growth and/or behavioral changes. Any such change is likely to alter interspecies interactions and hence community structure.

PREDATION ON OPPORTUNISTS

Hydroids are often one of the first groups of organisms to colonize disturbed or newly available surfaces (Harris and Irons, 1982). Many hydroids appear to follow the general pattern described for opportunists in community succession by Connell and Slatyer (1977); they may dominate space for a period, but they seldom replace themselves because succeeding generations fail to appear and they ultimately give way to later successional stage species.

The presence of hydroids can influence the sequence or species composition in the successional sequence. Standing (1976) found that colonies of *Obelia* inhibited the recruitment of barnacles because the polyps ate the cyprids and stolons interferred with settlement, while tadpole larvae of the tunicate *Mogula* were able to recruit successfully. The next stage of succession was altered from a barnacle-dominated system to one occupied by tunicates. Russ (1980) showed that tufts of string simulating hydroids facilitated the successful establishment of tunicates and bryozoans by protecting the young stages from fish predation. Dean and Hurd (1980) found that hydroids increased the recruitment of mussels onto fouling panels. In most cases, hydroids are described as being early colonists and being replaced without any information on why they do not persist or whether they can influence the succeeding stages of the community.

One reason why hydroids are unlikely to persist is the recruitment of aeolid and dendronotid nudibranch predators that ultimately consume the hydroids (Orton, 1914; Lagardere and Tardy, 1980; Harris and Irons, 1982). Even in algal-dominated communities, hydroids and nudibranchs may be one of the earliest ephemeral stages in community development. Within six weeks of a February, 1983 storm that caused high sea urchin mortality, facilitating the reestablishment of kelp beds in many communities along the coast of Southern California (Ebeling *et al.*, 1985; Harris *et al.*, 1984), many of the scoured surfaces at Naples Reef in the Santa Barbara Channel were covered with stolon networks of thecate hydroids. These hydroids were heavily infested with small aeolids including *Eubranchus* spp., *Cuthona albocrusta* (MacFarland), and *Hermissenda crassicornis* (Eschscholtz) (Harris, unpublished observations).

Nudibranchs in low densities are unlikely to seriously damage a hydroid colony since colonial forms grow at exponential rates while the individual nudibranch will feed at an arithmetic rate. Evidence from one study suggests that nudibranch predation may induce changes in hydroid growth form. Gaulin *et al.* (1986) showed that predation by the nudibranch *Tenellia adspersa* (Nordmann) caused an increased stolon budding rate in the hydroid *Cordylophora lacustris* Allman. The critical factor in inducing this change in growth form was a factor associated with *T. adspersa* mucous, because forceps and nudibranch mucous caused increased stolon budding while removal of polyps by forceps alone inhibited stolon budding completely. Nudibranch predation should result in a denser colony growth form in *Cordylophora.* Folino (1985) found indications of altered growth form in colonies of *Hydractinia echinata* (Fleming) in response to feeding by *Cuthona nana* (Alder and Hancock). If this phenomenon of altered growth from cropping nudibranch predation is widespread, it could influence the effectiveness of hydroid colonies as larval filters (Standing, 1976) and add a stochastic influence to subsequent community development. The induction of spines for defense by predator substances is already well-documented in other groups such as rotifers (Gilbert, 1980) and bryozoans (Harvell, 1984). Cropping by ungulates has been shown to stimulate certain grasses to form denser stands by vegetative growth (McNaughton, 1984; Belsky, 1986).

High densities of nudibranchs can result in the total destruction of a hydroid colony. The buildup of nudibranchs on a hydroid population is also likely to have a secondary impact, the inhibition of subsequent hydroid recruitment. New colonies of hydroids are unlikely to survive where a high density of nudibranchs is encountering a decreasing food source. The perisarcs of the initial colonies will remain after the polyps have been consumed much as the effect of defoliation of trees by herbivores. As with the remaining herbivores, the resident nudibranchs will inhibit the recruitment of new hydroid colonies of the same species. Clark and Clark (1984) reviewed the literature pertaining to the models proposed by Janzen (1970) and Connell (1971) to explain high tree species diversity in tropical rain forests. The model states that seeds and seedlings of rain forest trees will suffer highest mortality near adults of the same species due to an accumulation of herbivores associated with that species. Clark and Clark (1984) found that the literature relating to the Janzen-Connell Model was mixed, though generally supportive. While the mechanisms determining tropical rain forest tree species diversity are likely to be several and complex, the patterns of hydroid-nudibranch turnover suggest that the Janzen-Connell Model may be at least one mechanism explaining why hydroids generally do not replace themselves in early successional stage communities. Observations of algal dominated communities in the Gulf of Maine suggest that small herbivores such as the prosobranch *Lacuna vincta* (Montagu) may have a similar impact on early successional stage algae such as *Ulva* spp. and filamentous rhodophyta (Lubchenco, 1986; Harris, in press).

Hydroids with their arborescent growth forms and exoskeletal perisarc enhance topographic relief on new surfaces. The skeleton elevates the colony into the water column for feeding, but it also provides physical structure for setting nudibranchs and the larvae of later successional stage organisms such as mussels and tunicates (Standing, 1976; Harris and Irons, 1982; Dean and Hurd, 1980). The physical structure of opportunists may provide refuges from predators, both on micrograzers such as nudibranchs and the young stages of competitive dominants (Russ, 1980). It may be that opportunists such as hydroids and filamentous algae are their own worst enemies, because the physical structure provides settling surface and protection from predation for both their predators and competitors.

PREDATION ON LONG-LIVED SPECIES

Some cnidarians, such as sea anemones and corals, are long-lived and capable of assuming the role of competitive dominant in certain communities. Cloning sea anemones such as *Anthopleura elegantissima* (Brandt) and *Metridium senile* L. can dominate considerable space in intertidal and fouling communities respectively (Sebens, 1979; Hoffman, 1976; Harris and Irons, 1982). The aeolid nudibranch *Aeolidia papillosa* (L.) is a major predator on anemones in northern Atlantic and Pacific coastal environments. Schick *et al.* (1979) proposed that the population structure of *M. senile* at a site on the Maine coast was due to predation by *A. papillosa.* Studies by Harris on the West Coast (1976) and East Coast (1986) of the United States have shown that *A. papillosa* is a size-selective predator on *M. senile* due to the effectiveness of acontia extrusion as a defense by large anemones. Laboratory and field studies have shown that nudibranch predation is at least one mechanism that can account for some populations of *M. senile* being dominated by solitary and small aggregations of large individuals, while in areas of low nudibranch numbers, *M. senile* occurs in large clones dominated by small specimens (Harris, 1986).

A number of studies described chemotactic behavior in *Aeolidia papillosa* (Stehouwer, 1952; Braams and Geelen, 1953; Harris and Duffy, 1980; Hall *et al.*, 1982, 1984) and prey preference among a range of anemone species (Waters, 1973; Edmunds *et al.*, 1974, 1976; Harris and Howe, 1979; Hall *et al.*, 1982, 1984; Hall and Todd, 1986; Harris and Duffy, 1980; Harris, 1986). Ingestive conditioning (Wood, 1968) has been demonstrated by Hall *et al.* (1982) and Harris and Duffy (1980), but Hall *et al.* (1984) were not able to conclusively show switching behavior (Murdoch, 1969). A conflict over whether *Metridium senile* is a preferred prey of *A. papillosa* has been evident in the literature for some time with most prey-selection experiments tending to suggest that *A. papillosa* does not prefer *M. senile* (Waters, 1973; Edmunds *et al.*, 1974, 1976; Harris and Howe, 1979; Hall *et al.*, 1982, 1984; Hall and Todd, 1986). However, *A. papillosa* is found associated with *M. senile* in both the Pacific and Atlantic Oceans (Harris, 1973, 1976, 1986) and does show a preference for *M. senile* in olfactometer tests when fed small individuals of the anemone (Harris and Duffy, 1980). The apparent conflict seems to be due to the fact that most investigators use larger sized individuals of *M. senile* which have an effective defense in acontia extrusion that is most effective under laboratory conditions (Harris, 1986).

Nudibranch predation on anemones makes space available on hard substrata both by consumption of anemones and by escape responses such as crawling (Edmunds *et al.*, 1976; Harris and Howe, 1979), swimming (Robson, 1966; Harris, 1973) or releasing from the substratum (Rosin, 1971; Harris, 1973; Edmunds *et al.*, 1976). Cloning anemones such as *Metridium senile* are effective space occupiers and may be competitive dominants in fouling communities or on undercut surfaces in the rocky subtidal (Harris and Irons, 1982; Harris, 1986). The disturbance caused by nudibranch predation opens space for other species to recruit, thereby potentially increasing diversity in these communities. Anemone-eating nudibranchs can, therefore, serve a similar function in fouling communities to that of *Pisaster* in the rocky intertidal, a keystone predator (Paine, 1966). It may be stretching the point to claim that aeolid nudibranchs are keystone predators, but some species are capable of preventing space monopolization by certain anemones. *Coryphella salmonacea* (Couthony) in the Gulf of Maine (Morse, 1971) and *Hermissenda crassicornis* in California (Harris, personal observation) feed on colonial tunicates that can become major space occupiers. However, the most likely nudibranchs to have a major impact on the climax communities of many fouling and cryptic communities are the large sponge-eating dorids so prevalent in some regions, since sponges have the potential to be very effective long-term space competitors (Harris and Irons, 1982; see Wells *et al.*, 1964).

AEOLID NUDIBRANCHS AS PREY

There has been much speculation about predation on nudibranchs, presumably because there are a number of large, brightly colored species that wander about in the open without being attacked. A number of authors have offered nudibranchs to fish with the result that the nudibranch is grabbed, mouthed and rejected (Harris, 1973; Todd, 1981). In his detailed study of aeolid nudibranch secretory glands and cnidosacs, Edmunds (1966) concluded that predation by visual hunters must have been a strong evolutionary selective pressure.

Several predators of nudibranchs have been identified. Paine (1963) conducted extensive prey preference studies on the cephalospidean *Navanax inermis* (Cooper) and showed that it will eat many species of nudibranchs including aeolids.

The notaspidean *Pleurobranchaea californica* (Dall) will eat a number of aeolid and other nudibranchs (Harris, unpublished observations). In the Pacific Northwest, the seastar *Crossaster papposus* (L.) readily feeds on nudibranchs (Mauzey *et al.*, 1968), but eats seastars in the Atlantic (Hancock, 1955; Hulbert, 1980). Various crabs and lobsters have been cited as potential predators, but there is little evidence (Harris, 1973; Todd, 1981). Fish predation has received the most attention, presumably due to the conspicuous coloration of many nudibranchs and the fact that fish are visual predators.

Todd (1981) reported that wrasses ate small aeolids and saccoglossans exposed when coral heads were overturned in the Red Sea. Harris (1973) proposed that fish predation must be important as a selective force based on studies of two species of aeolids in the coral-eating genus *Phestilla*. Both species are cryptic in coloration and behavior, deriving their coloration from coral pigments and/or zooxanthellae. Neither species of *Phestilla* stores nematocysts from their coral prey, apparently because coral nematocysts are no protection against the numerous fish species that actively feed on corals. The cnidosacs in *Phestilla* spp. have become secretory glands (Harris, 1973). Harris (1986) reported on fish predation on the dorid *Onchidoris bilamellata* (Alder and Hancock) and the aeolid *Aeolidia papillosa*. Both species were found in the stomach contents of large (> 30 cm) specimens of the winter flounder *Pseudopleuronectes americanus* (Walbaum).

Harris (1986) also conducted field and laboratory studies of predation by the wrasse *Tautogolabrus adspersus* (Walbaum) on the aeolid *Aeolidia papillosa*. The results showed that *T. adspersus* does eat *A. papillosa*, but that the relative sizes of predator and prey are important, with the fish taking smaller size classes. Since *A. papillosa* is seldom common, most of the fish predation must be both size-selective and investigative in nature. *A. papillosa* is least common among *Metridium* populations where fish are aggregated such as caves, breakwaters and pilings, and more common in open habitats where fish are uncommon (Harris, 1986). It appears that the presence of wrasses has a negative impact on *Aeolidia* recruitment to those sites where fish are common and this allows the development of large aggregations of small-sized *Metridium*. In contrast, the absence of fish allows a buildup of *Aeolidia:* being a size-selective predator on *Metridium,* this could result in scattered populations of anemones dominated by large individuals.

COLORATION AND MIMICRY

Aeolidia papillosa is brownish in color with some populations having a white mottling. Individuals are nocturnal and tend to hide or remain in a contracted state during the day. The larger contracted individuals closely resemble a sea anemone with their many cerata looking like tentacles. It is clear that *Aeolidia* is cryptic in form, coloration and behavior. At the opposite extreme are species such as *Hermissenda crassicornis* of the West Coast of the United States which are large, strikingly colored and conspicuously active by day. The question of whether an aeolid is cryptic or aposematic must include the size, habitat and behavior of the species, as well as the possession of a noxious defense.

It is most likely that all aeolids less than 10 mm are cryptic due to their size and the heterogeneous nature of the background represented by most assemblages of benthic organisms (see Edmunds, 1974). This would be similar to a skunk that is cryptic at a distance in the mosaic of shadows and moonlight in a temperate woodland at night when skunks are active. Even the striking patterns of many small aeolid species blend with the background and these species are seldom found away from their hydroid prey. For those species that do grow beyond 10 to 15 mm, most appear to remain cryptic due to a combination of coloration and nocturnal or inconspicuous behavior. Over half of the aeolid species known from the Gulf of Maine are crytic due to size, coloration and behavior as adults (Harris, unpublished observations) while at least 25 of the 35 species of aeolids reported from the West Coast by Behrens (1980) and McDonald and Nybakken (1980) are apparently cryptic.

Species that are aposematic in coloration and behavior such as *Coryphella verrucosa* (Sars) in the Gulf of Maine and *Hermissenda crassicornis* are distasteful to fish and avoided. Wrasses that readily fed on *Aeolidia papillosa* would not touch *C. verrucosa* (Harris, 1986). Efforts to induce feeding of wrasses and surfperch on *Hermissenda* at Naples Reef in the Santa Barbara Channel were fruitless, even though numerous smashed sea urchins were placed among the nudibranchs, the fish actively selected the pieces of urchin without touching the nudibranchs. In a similar test the same species of fish consumed individuals of the cryptic *Dendronotus frondosus* (Ascanius), *Hancockia californica* MacFarland and *Elysia* sp. with minimal stimuli from broken urchins (Harris, Lambert and Laur, unpublished observations).

If warning coloration does occur in some aeolid nudibranchs, then it is possible that mimicry could occur in some groups (Wickler, 1968; Edmunds, 1974). Of the two major forms of mimicry, Batesian and Müllerian, the latter seems more likely since many species have arrays of secretory glands that appear to be defensive in function (Edmunds, 1966; Harris, 1973; Todd, 1981) and almost all aeolids store nematocysts. One possible example of Batesian mimicry could involve the aeolid *Hermissenda crassicornis* (which does apparently have warning coloration) and the arminid *Antiopella barbarensis* (Cooper). *Antiopella* has a similar morphology and coloration, though it eats bryozoans and does not store nematocysts. It could be that *Antiopella* and *Hermissenda* are equally distasteful, but no work has been done on this species. The author has observed numerous co-occurring specimens of these two species in the intertidal at Dillon Beach, California. The cerata of both species were yellowish in color and it required careful inspection to tell them apart.

Rudman (1982, 1983) has documented the regional occurrence of species complexes of tropical dorids from several genera. Each grouping of species has a distinct color pattern making identification of live specimens difficult. Most of the species are in the genus *Chromodoris*, all of which tend to have large marginal secretory glands that are presumably defensive in nature. This appears to be an example of Müllerian mimicry similar to the complexes of distasteful butterflies described from the tropics (Wickler, 1968; Edmunds, 1974). Goddard (1987) suggested that the dorids *Crimora coneja* Marcus, *Laila cockerelli* MacFarland and *Triopha catalinae* (Cooper) from the coast of California could form a mimicry complex, but was unsure whether it would be Mullerian or Batesian.

A possible example of Müllerian mimicry in aeolid nudibranchs exists in the Gulf of Maine on the east coast of the United States. In the region, there is a low diversity of epibenthic feeding fish (Bigelow and Schroeder, 1953), with the wrasse *Tautogolabrus adspersus* being the most obvious. There is also a low diversity of known nudibranch species (Harris, 1973; Gosner, 1971) with the present known number being 32. There are 13 species of aeolids that have a broadly similar color pattern of reddish ceratal digestive diverticula with white tips [*Cuthona concinna* (Alder and Hancock), *C. nana, Catriona gymnota* (Couthony), *Eubranchus tricolor* Forbes, *E. sanjuanensis* Roller, *Facelina bostoniensis* Couthony, *Setoaeolis pilata* (Gould), *Coryphella verrucosa, C. verrilli* Kuzirian, *C. salmonacea, C. nobilis* Verrill, *C. gracilis* (Alder and Hancock), *C. pellucida* (Alder and Hancock)]. This species complex comprises 40% of the nudibranch fauna in the southern Gulf of Maine. The wrasse *T. adspersus* rejects *C. verrucosa* which is one of the most common large aeolids in the region and this nudibranch may serve as the model. It could be that the low diversity of visual predators in this region has led to one conspicuous color pattern being selected for. Mimicry in nudibranchs could be far more common than realized and nudibranchs could prove to be excellent models for the study of visual predation as a selective force on the evolution of marine invertebrates.

CONCLUSIONS

The biology and autecology of aeolid nudibranchs has become increasingly well documented (see McDonald, 1986), but little is known about the roles played in marine benthic communities by this common group of molluscs. Aeolids are among the most common predators on cnidarians which are conspicuous occupiers of primary space in the successional sequences of many hard substratum communities and we know little about the contributions of either predator or prey. The processes in which they are participating are often dynamic and take place at rates faster than the sampling periodicities of most ecological studies. The advantage of this fast turnover time is the possibility of conducting short-term experiments that have the potential of providing insights into the mechanisms that determine the patterns observed over longer time scales.

Hermissenda crassicornis and *Aeolidia papillosa* provide just two examples of species that have interesting possibilities for ecological study. *Hermissenda* beings life as a micrograzer on ephemeral hydroids such as *Obelia* (Harrigan and Alkon, 1978). It is cryptic and is one of a suite of species that ultilmately overwhelms the established colonies and could prevent recruitment of more colonies of the same species. *Hermissenda* grows to greater than 40 mm in length and assumes the role of predator not only on hydroids, but also on small hydroid-eating aeolids as well as colonial tunicates that are space competitors in later successional stage fouling communities. *Hermissenda* is diurnal and aposematic in coloration and behavior; it could also serve as a model for mimicry from at least one nudibranch species that is not even an aeolid. *Aeolidia papillosa* is a specialist on sea anemones at all stages of its benthic existence. It is cryptic in coloration, behavior and probably morphology with its prey anemones serving as models. *Aeolidia* could play a role not unlike a keystone predator by opening space in anemone aggregations and, therefore, preventing space monopolization by species that are capable of being effective space competitors.

This review of information relating to the roles of aeolid nudibranchs in marine benthic communities is designed to stimulate discussion and suggest gaps in our knowledge that require our attention rather than to provide definitive answers. It is hoped that more detailed study of aeolid nudibranchs as both predators and prey will not only add to our knowledge of the group, but will help us to understand the processes by which marine benthic communities function.

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